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DARWIN'S THEORY OF EVOLUTION BY THE SELECTION OF MINOR SALTATIONS

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There is an opinion which is becoming more widely prevalent daily that Charles Darwin's theory of selection rests upon "fluctuations" which may not be heritable. Nothing could be further from the facts.[1]

It is true that Darwin finally came to believe in the inheritance of somatic modifications (in the modern sense of bodily changes) caused by the direct action of environment as well as by habit (ontogeny), but in his original (1859) and final (1872) opinion evolution was *chiefly* due to the selection of heritable "individual differences."

Darwin's true meaning as to *"individual differences"* is not to be found in his language, but in the *cases* he cited; he has been widely misunderstood[2] as believing in continuous evolution whereas he chiefly believed in discontinuous evolution.

Darwin's final opinion[3] may be cited with a transposition of sentences and italicizing of important words, as follows:

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[1] De Vries is partly responsible for this general misunderstanding of Darwin. In "Die Mutationstheorie," Leipzig, 1901, pp. 21–27, we find a very full discussion of the opinions of Darwin in which the interpretation is reached that Darwin was not clear in distinguishing "variation" and "mutation."

[2] Cox, Chas. F., "Charles Darwin and the Mutation Theory," *Ann. N. Y. Acad. Sci.*, Vol. XVIII, No. II, Pt. III, February 10, 1909, pp. 431–451. This is a most conscientious and exhaustive review of Darwin's opinions in which the following conclusion is reached: "As we have seen, he was compelled to concede that what we now call mutation had occasionally taken place and become the starting point of new races, but he was none the less unshaken in the conviction that this process was exceptional and extraordinary, and that, as a rule, a new species originated by the gradual building up of minute and even insignificant deviations from the average characters of an old species, *which deviations we now call fluctuations.*" [P. 450, italics our own.]

[3] "The Variation of Animals and Plants under Domestication," Vol. II, p. 397.

> . . . we have abundant evidence of the constant occurrence under nature of slight individual differences of the most diversified kinds; and we are thus led to conclude that species have generally originated by the natural selection of extremely slight differences. This process may be strictly compared with the slow and gradual improvement of the racehorse, grayhound, and gamecock. As every detail of structure in each species has to be closely adapted to its habits of life it will rarely happen that one part alone will be modified; but as was formerly shown, the co-adapted modifications need not be absolutely simultaneous. Many variations, however, are from the first connected by the law of correlation. Hence it follows that even closely allied species rarely or never differ from one another by one character alone . . . from the history of the racehorse, grayhound, gamecock, etc., and from their general appearance we may feel nearly confident that they were formed by a slow process of improvement; and we know that this has been the case with the carrier-pigeons as well as with some other pigeons. . . . It is certain that the ancon and mauchamp breeds of sheep, and almost certain that the niata cattle, turnspit, and pug dogs, the jumper and frizzled fowls, short-faced tumbler pigeons, hook-billed ducks, etc., suddenly appeared in nearly the same state as we now see them. So it has been with many cultivated plants. The frequency of these cases is likely to lead to *false* belief that natural species have often originated in the same abrupt manner. But we have no evidence of the appearance, or at least of the continued procreation, under nature, of abrupt modification of structure, and various general reasons will be assigned against such a belief.

Thus Darwin, on the admirable ground that *no evidence had been adduced in nature* of such transformation, rejected the hypothesis of major saltatory evolution as causing the *natural* appearance of entirely new types of animals or plants or of entirely new and profoundly modified organs. There was no evidence in 1872 and there is none to-day of the sudden appearance in nature of such a breed as the ancon sheep. On the other hand, Darwin's meaning as to *"slight individual differences of the most diversified kinds,"* as clearly conveyed in the hundreds of observations he cited in "The Origin of Species" (edition of 1872) and especially in his "Variation of Animals and Plants Under Domestication," is *that such individual differences were in the nature of minor saltations of character, structural or functional, and always hereditary.* Since Darwin observes that *natural selection may be strictly compared with the slow and gradual improvement of the racehorse, grayhound,* etc., if we collect all the observations which he assembled as to the genesis of the racehorse and grayhound we may gain a concrete understanding of his opinions as to the genesis of species. It will appear that many of the *new characters* which Darwin cites, and he used the term "new characters" interchangeably with "individual differences," are clearly identical with minor saltations or with the "mutations of De Vries," as generally understood by zoologists to-day.

"We may therefore conclude," observes Darwin,[4] "that, whether or not the various existing breeds of the horse have proceeded from one or more aboriginal stocks, yet that a great amount of change has resulted from the direct action of the conditions of life, and probably a still greater amount from the long-continued selection by man of slight individual differences." Among the examples he cites in amplification of this conclusion are the following:

(1) Eight incisors or two super-normal; (2) canines in females; (3) a nineteenth or posterior rib; (4) a supplementary hock-bone; (5) a reversional trapezium and Mtc.V; (6) horn rudiments in the frontal bones one or two inches in length; (7) tailless foals which, he observes, might have produced a new breed; (8) curled hair correlated with short manes and tails and mule-like hoofs.

All the above "individual differences" are cited by Darwin as hereditary; all are "discontinuous" in Bateson's sense or "mutations" in De Vries's sense. In other parts of Darwin's works most of the numerous references made to "individual variations" in horses are of the same character, namely, saltatory and hereditary. Although (5) cited above is a "reversion," reversions and ontogenic modifications are, for the most part, clearly distinguished as belonging to another category.

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[4] "Animals and Plants under Domestication," Vol. I, p. 55.

Similarly Lutz[5] has kindly analyzed for the writer twenty-one cases cited by Darwin among insects as possible material for selection and as indicating modifications by environment. Eight of these cases are doubtful; seven cases represent "gradations," or "slow degrees," probable or possible continuity; six cases represent discontinuity. It seems to Dr. Lutz that Darwin made the most of the cases of discontinuous variation he knew about, but that for the most part he had continuous variation in mind.

It is therefore of interest, in view of the neglectful and almost contemptuous attitude of certain writers toward Darwin's observations, to make a fresh summary of the principles found scattered through the pages of his great work on "Variation," reexpressing some of these principles in modern terms.

Darwin on "New Characters" and "Individual Differences"[6] as Expressed in Modern Terms

(1) Newly appearing characters arise from unknown causes, either stable in heredity, variable in heredity, or not hereditary at all.[7] (2) "Individual variations" are minor suddenly appearing characters, heritable. (3) Characters of all kinds, whether new or old, tend to be inherited. Those which have already withstood environment will, as a rule, continue to withstand it and be truly transmitted. (4) A change of environment is principally but not invariably the source of new variations. (5) There are periods of variability or mutability in which many new characters appear. (6) New characters are observed to accumulate in successive generations in the

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[5] Frank E. Lutz, letter to the writer, December 15, 1911, "References to insects in the 'Origin of Species,' especially those bearing on the question of continuity *versus* discontinuity."

[6] See American edition, 1900, "Animals and Plants under Domestication," dated by Darwin January, 1872.

[7] Vol. II, p. 37.

same direction. (7) There is a predisposition to similar progressive variations in descendants of one stock (termed "analogous or parallel variation") due to unknown causes acting on similarly constituted organisms.[8] (8) There is a marked prepotency in heredity in saltatory types, *e. g.,* ancon sheep, turnspit dogs. (9) There is "in a certain sense" a mosaic inheritance (after Naudin) observed in hybrids, or character segregation by self attraction and self affinity. Similarly there is an exclusive inheritance, as observed in characters derived exclusively from the father or mother and lying dormant or latent for many generations. (10) There is a particulate inheritance, for example, of the special quality of vigor and endurance observed in descendants of the racehorse "Eclipse"; *i. e.,* a dominance of single characteristics. (11) A large number of individual variations cited are antithetic characters rather than slight or infinitesimal gradations of similar characters, *e. g.,*

Erect ears	Drooping ears
Fertility	Sterility
Immunity	Non-immunity
Resistance to environment	Non-resistance to environment

(12) Environment directly affects the antithetic characters of sterility and fecundity. (13) New characters may appear and old ones disappear at any stage of development.[9] (14) There is a similar age heredity or inheritance at corresponding periods of life. (15) There is a sex-limited heredity. (16) There is a correlated variability or coupling of new characters in heredity, *e. g.,* black color of the skin and immunity from disease. (17) Particulate inheritance as shown in non-blending colors, *e. g.,* gray and white mice produce piebald young, or gray or white young, but never a blend between gray and white. (18) Old characters lying latent are ready to be evolved under certain old environmental conditions. Thus we observe the ontogenic revival of feral characters

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[8] Vol. II, p. 329.

[9] Vol. II, p. 392.

in feral environment, and of domesticated characters in return to domestication, *e. g.,* barking in dogs. (19) Ontogenic reactions to environment are observed in all external and internal characters in animals and plants. (20) Under *selection* Darwin anticipated the theory of organic or coincident selection.[10]

SUMMARY

Darwin did not so sharply distinguish in *language* as Weismann and Mendel have taught us to between the different kinds of variation and different factors of evolution, yet in his observations and the cases he cites his perception is absolutely clear between *heredity, ontogeny, environment* and *selection* as interoperating factors. In fact, he remarks[11] on the frequent difficulty of distinguishing between the inextricably mingled factors of ontogeny (*e. g.,* effects of use and disuse), and of correlated or coadapted variability and of spontaneous variations. A comparison of all the various kinds of variation cited by Darwin in his two great volumes shows that they fall into the following four classes:

I. ''Individual variations,'' ''spontaneous variations,'' new suddenly appearing heritable characters, practically equivalent to the minor mutations of De Vries, believed by Darwin to be the chief material of natural selection and evolution.

II. Sports, or major saltations, such as the ''mauchamp,'' ''ancon'' and ''niata'' breeds, believed by Darwin not to occur in a state of nature.

III. Fluctuations of proportion, congenital and hence transmissible, equivalent to the quantitative variation of Bateson, best illustrated by Darwin in his theory of the evolution of the long neck of the giraffe:

> So under nature with the nascent giraffe, the individuals which were the highest browsers, and were able during dearths to reach even an inch or two above the others, will often have been preserved; for they

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[10] Vol. II, pp. 317, 318.

[11] Vol. II, p. 327.

will have roamed over the whole country in search of food. That the individuals of the same species often differ slightly in the relative lengths of all their parts may be seen in many works of natural history, in which careful measurements are given. These slight proportional differences, due to the laws of growth and variation, are not of the slightest use or importance to most species. But it will have been otherwise with the nascent giraffe, considering its probable habits of life; for those individuals which had some one part or several parts of their bodies rather more elongated than usual, would generally have survived. These will have intercrossed and left offspring, either inheriting the same bodily peculiarities, or with a tendency to vary again in the same manner; whilst the individuals, less favored in the same respects, will have been the most liable to perish.

IV. Fluctuating variability, clearly distinguished by Darwin from II and not especially connected by him with the process of evolution.

December 30, 1911